Response of soil microbial and invertebrate communities to tracked vehicle disturbance in tallgrass prairie ☆

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ABSTRACT

Soil biota drive fundamental ecosystem processes such as decomposition, nutrient cycling, and maintenance of soil structure. They are especially active in grassland ecosystems such as the tallgrass prairie, where much of the net primary productivity is allocated belowground and ultimately processed by heterotrophic soil organisms. Because both soil microbes and soil fauna display perturbation responses that integrate the physical, chemical, and biological changes to their environment, the structure of belowground microbial and faunal communities is used widely as an indication of the ecological status of soils. To investigate the effects of military training on tallgrass prairie soil communities, a replicated small-plot study of tracked vehicle disturbance effects was initiated at Fort Riley, Kansas in 2003. This article reports subsequent rates of recovery for soil microbial and invertebrate communities over a range of disturbances encompassing different soil types (silty clay loam and silt loam soils), environmental conditions (wet vs. dry traffic events), traffic intensities (single vs. repeated traffic), and track areas (curve vs. straightaway). Microbial biomass in wet silty clay loam soil treatments and on curve areas in silt loam soil was suppressed for 1–2 years following disturbance but increased to levels greater than undisturbed plots in all treatments by the fourth year. Nematode abundance, family richness, trophic composition, and community structure also displayed maximum disturbance for wet treatments and curve areas. Trophic composition and community structure continued to exhibit disturbance effects throughout the 4-year study period, even after recovery of nematode abundance. Earthworm abundance displayed the most severe reductions (78% across soil types, treatments and areas) immediately following tank traffic but, like microbial biomass, subsequently increased to levels greater than undisturbed plots. Nematode community structure provided a reliable and comprehensive assessment of the status of the soil food web and was an effective bioindicator of ecosystem recovery following traffic disturbance. In addition, given the dominant role of earthworms in ecosystem processes and their extreme sensitivity to tracked vehicle disturbance, it is recommended that this group be included in monitoring protocols for military training land managers.

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1. Introduction

Soil biota are important drivers of fundamental ecosystem processes such as decomposition, nutrient cycling, and maintenance of soil structure. In grassland ecosystems, where much of the net primary productivity is allocated belowground and ultimately processed by heterotrophic soil organisms, their importance is amplified (Elliott et al., 1988). The tallgrass prairie, in particular, is characterized by high belowground productivity and large accumulations of soil organic matter and nutrients resulting in a large and diverse assemblage of soil biota (Ransom et al., 1998; Rice et al., 1998). Ecosystems display characteristic structural and functional signatures in soil communities, suggesting that the biological status of soils reflects soil quality as well as overall ecosystem health (Ritz et al., 2004). Indeed, the structure of belowground microbial and faunal communities has been used widely as an indication of the ecological status of soils (Linden et al., 1994). Soil fauna provide several advantages over microbial communities, however, because they reflect higher trophic levels in the soil food web, generally are easier to assess, and their populations are relatively stable (Neher, 2001). Nematodes are among the most popular soil faunal indicators because they represent a comprehensive array of functional or trophic groups occupying multiple positions in the soil food web (Yeates et al., 1993).

Soil macroinvertebrates such as earthworms play a dominant role in ecosystem processes, making them particularly significant indicators of soil health. Earthworm burrowing and feeding activities result in improved aeration and water infiltration, incorporation of organic matter into the soil, and stabilization of soil aggregates (Tomlin et al., 1995; Edwards and Bohlen, 1996), leading to their designation as 'ecosystem engineers' (Jones et al., 1994). The tallgrass prairie soils of the Flint Hills region of eastern Kansas contain a mixture of native and exotic earthworm species which together account for most of the faunal biomass (James, 1995; Rice et al., 1998). Departures from historical disturbance regimes of frequent fire and grazing facilitate the expansion of exotic earthworms, possibly with the displacement of native species (Callaham and Blair, 1999; Callaham et al., 2003).

There is a clear need for the further identification and development of biological indicators for soil quality (Loveland and Thompson, 2001; Ritz et al., 2004). Belowground systems exhibit great complexity, with extremely high levels of biological diversity, although it is the functional aspects of these systems that appear to be the most descriptive (Ritz et al., 2004). Since the complexity of soil communities is related largely to the spatial heterogeneity and diversity of resources (Maire et al., 1999), disturbance of soil physical and chemical properties are expected to have profound effects on both their structure and function. The rate of recovery in community structure and/or function following such perturbation provides a useful indicator of soil and, therefore, ecosystem resilience (Ritz et al., 2004).

Mechanized military training provides a dramatic example of landscape-scale soil disturbance, impacting soil quality in multiple ways, most notably through displacement and compaction. The environmental impacts of military vehicle use on natural areas have been reviewed recently by Anderson et al. (2005). While numerous studies have identified ecological processes sensitive to military training activities, additional research is needed to identify soil quality-related indicator variables for inclusion in monitoring programs on military lands. Fort Riley Military Installation, located in the Flint Hills of northeastern Kansas, is the site of ongoing research on the effects of military training on the mesic tallgrass prairie ecosystem. Fort Riley is a major training reservation, with seventy percent of its 40,434 ha used for mechanized maneuvers. In an early comparison of training sites on Fort Riley with an undisturbed, native tallgrass prairie site, soil invertebrates, including macro- and microarthropods, and native earthworm species, were identified as sensitive indicators of compaction resulting from mechanized maneuvers, even in the absence of observable effects on plant productivity (Schaeffer et al., 1990). A subsequent landscape-scale evaluation on Fort Riley identified nematode family richness as a strong indicator of disturbance due to mechanized maneuver training (Althoff et al., 2007). Althoff (2005) monitored the status of soil microbial and invertebrate communities following M1A1 tank traffic disturbance during wet and dry conditions in two soil types on Fort Riley and observed dramatic reductions in both the abundance and richness of macroinvertebrate and nematode assemblages. Earthworms were the most sensitive group, with reductions in numbers approaching 100% in plots with the maximum disturbance regime.

Land maintenance on military training lands is currently guided by regulations set forth by the integrated training area management (ITAM) Program, which outlines procedures for achieving sustainable use of training lands (Army Regulation 350-4, 1988). A key component of this program, range and training land assessment (RTLA), provides information and recommendations to range managers regarding the condition of training lands to assist scheduling of training areas and monitoring of the effectiveness of rehabilitation projects (US Army Environmental Center, 2006). Fort Riley started implementing portions of the assessment protocol under the land condition trend analysis (LCTA) Program, monitoring trends in plant communities related to military vehicle traffic patterns during 1994–2001 (Althoff et al., 2006). Assessment of soil quality indices, including physical, chemical, and biological properties began in 2002 (Althoff, 2005; Althoff and Thien, 2005; Althoff et al., 2007).

A replicated small-plot study of tracked vehicle disturbance effects on tallgrass prairie soils and communities was initiated on Fort Riley in 2003. The objectives were to evaluate rates of recovery in a suite of plant and soil-quality indicators over a range of disturbances encompassing different soil types, environmental conditions, and traffic intensities. Results from the first two years are reported in Althoff (2005) and Althoff and Thien (2005). This manuscript reports longer-term trends in recovery of soil biota subsequent to military training disturbance.

2. Materials and methods

2.1. Site description

Research was conducted at Fort Riley Military Installation, an Army base in operation since 1853, located in Clay, Geary, and Riley counties in the Flint Hills of northeastern Kansas (39°15′N, 96°50′W) (Pride, 1997; McKale and Young, 2000). The installation, located in a mesic, tallgrass-prairie ecosystem, uses 29,542 ha of its 40,434 ha for maneuver training. The Flint Hills grasslands encompass more than 1.6 million ha, covering much of eastern Kansas from near the Kansas-Nebraska border south into northeastern Oklahoma, and contain the largest remaining areas of untilled tallgrass prairie in North America (Knapp and Seastedt, 1998). Hot summers and cold, dry winters characterize the climate. Mean monthly temperatures range from $-2.7\,°C$ in January to $26.6\,°C$ in July. Annual precipitation averages 835 mm, with 75% of precipitation occurring during the growing season (Hayden, 1998). Three major vegetative communities are found at Fort Riley: grasslands (ca. 32,200 ha), shrublands (ca. 6,000 ha), and woodlands (ca. 1,600 ha). The soil at the study plots was classified as a Wymore series consisting of very deep, moderately drained, slowly or very slowly permeable soils that formed in loess (Jantz et al., 1975). This soil series is found on most of the fort's training area. Wymore soils are classified as fine, smectitic, mesic Aquertic Argiudolls.

2.2. Experimental treatments

A randomized complete block design composed of three treatments (a non-trafficked control, tank traffic during wet soil conditions, and tank traffic during dry soil conditions) and three replications (blocks) was established in each of two soil types, a silty clay loam and a silt loam, in 2003 (Althoff and Thien, 2005). An Abrams M1A1 main battle tank created disturbances by driving five circuits around a figure eight pattern in designated plots either during wet or dry soil conditions. The M1A1 weighs 57.2 t with a ground pressure of 0.96 kg cm^{-2}. The tracks are approximately 63.5 cm wide and 4.57 m long. It has a maximum cross country speed of 48 km h^{-1}. Tank speed was maintained at approximately 8 km h^{-1}. Treatment during wet soil conditions occurred at soil saturation (gravimetric water content of ~30% for both soils). Treatment during dry soil conditions occurred at a gravimetric water content of 8% for both soils.

In 2004, one-half of each of the previously disturbed plots received five additional tank passes during wet or dry conditions similar to 2003. On a randomly selected half of the original figure eight, five additional passes were made with an M1A1 tank, producing an S-shaped pattern (Althoff, 2005). This second year of treatments allowed comparison of different levels of traffic

intensity (one-time-traffic with 5 passes versus repeated traffic with a total of 10 passes). Two areas, a curve and straightaway, within each traffic intensity subplot were designated for sampling in 2005. Data from the first and second years of disturbance are reported in Althoff (2005) and Althoff and Thien (2005).

In April 2006, each whole plot was again split and a randomly selected half received a burn treatment (Althoff, 2007). Curve and straightaway areas within each burn-intensity subplot were designated for sampling in 2006 and 2007.

2.3. Field sampling and laboratory methods

Bulk soil samples for microbial and soil invertebrate community analyses were collected following tank disturbance in May and July (wet treatment) and August and October (dry treatment) for 2003 and 2004, respectively. Subsequent samples were collected in November 2005, September 2006, and June 2007. A 20×50 cm Daubenmire frame (Daubenmire, 1959) was positioned at each sampling area (curve and straightaway) and the soil was removed to a depth of 7.6 cm, placed in a 22 l plastic bucket and covered with a lid. Samples were stored at $5\,°C$ ($41\,°F$) until further processing. All samples from disturbed areas were collected from the track pad, while control samples were collected from the undisturbed soil surface of control plots. Sampled depth, therefore, did not represent the same portion of the disturbed and undisturbed soil profiles.

2.3.1. Microbial biomass analysis

Microbial biomass was determined in the Microbial Lab, Department of Agronomy, Kansas State University using the fumigation-incubation technique described by Jenkinson and Powlson (1976). Bulk soil samples were mixed uniformly, and two 25 g subsamples were collected from each. One set was fumigated with chloroform and the other set was left unfumigated. The samples were incubated in 1 L mason jars for 10 days, and the CO_2 C concentration was measured using a Shimadzu GC-8A gas chromatograph. Nitrogen (NH_4 and NO_3) was extracted with 1 M KCL and analyzed on an Alpkem Autoanalyzer.

2.3.2. Soil invertebrate community analyses

Earthworms were hand-sorted, killed in boiling water, placed in 37% formalin for 2 days to set the proteins, and preserved in 70% ethanol for subsequent identification. Nematodes were extracted from $100\,cm^3$ soil subsamples by using a standard centrifugal-flotation technique (Jenkins, 1964) and identified to the family level to estimate family richness as an indicator of diversity. In addition to total abundance and family richness, a structure index and enrichment profile were constructed according to Ferris et al. (2001) and Ferris and Bongers (2006), respectively. The structure index is an indicator of the contribution of higher trophic levels to the soil food web and the enrichment profile depicts the proportional contribution of the total nematode community to plant, fungal, and bacterial channels. Both of these community indices provide a tool for monitoring the structure and function of the soil food web.

2.4. Statistical analyses

A disturbance effect index was calculated for all variables using the following formula:

(disturbed measurement-undisturbed measurement)/(disturbed measurement).

This disturbance effect index was expressed as a percentage of the control and subjected to mixed-model analysis of variance using SAS (SAS Institute, Cary, NC, 2000). The data were analyzed as a split-split plot with correlated subplots (5 passes vs. 10 passes) and correlated sub-subplots (curved vs. straight areas) with each subplot using a repeated measures analysis of variance modeling time (i.e. year) as a

regression variable. Models were constructed according to Littell et al. (1996) using SAS PROC MIXED. Linear and quadratic effects were tested and, where quadratic effects were not significant, a linear model was fit to the data. Slopes were compared among experimental treatments, and an equal slope model was fit where appropriate (i.e. where slopes did not vary among treatments). The significance of model estimates (based on deviation from undisturbed plots) was tested using least squares means (H_0: estimate = 0). Since the fire treatment was not implemented until 2006, burning was not included in the regression analyses, but the disturbance indices for burned and unburned plots were expressed relative to burned and unburned control plots, respectively, for 2006 and 2007.

3. Results

3.1. Microbial biomass

Microbial biomass C in undisturbed control plots during 2003–2007 averaged 702 (233–1314) $\mu g\,g^{-1}$ soil for the silty clay loam site and 838 (318–1235) $\mu g\,g^{-1}$ soil for the silt loam site. Microbial biomass N in undisturbed control plots during this same period averaged 168 (16–266) and 219 (149–277) $\mu g\,g^{-1}$ soil for silty clay loam and silt loam soils, respectively.

Modeling microbial biomass C as a polynomial function of time indicated a significant effect ($P \leq 0.05$) of soil moisture condition during tank traffic on both the initial level of disturbance and on subsequent linear trends in microbial biomass recovery, but only for the silty clay loam soil (Tables 1 and 2). Traffic effects on microbial biomass C were greater ($P \leq 0.01$) for disturbance during wet compared to dry soil conditions, with regression models predicting an initial reduction in microbial biomass C of 40% for tank traffic during wet soil conditions but little effect (17% increase) for tank traffic during dry soil conditions compared to that of undisturbed plots (Table 3, Fig. 1A). Actual observed impacts ranged from a
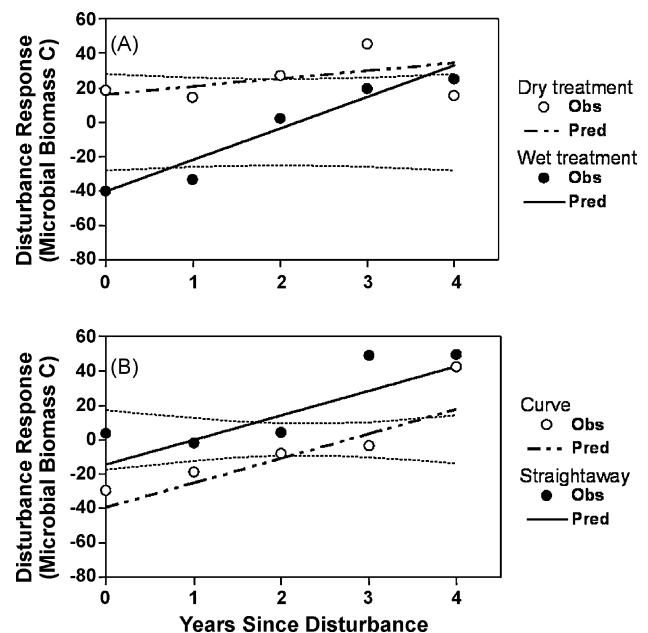
Fig. 1. Recovery trends for microbial biomass C following Abrams M1A1 Main Battle Tank traffic (A) during wet and dry soil moisture conditions in silty clay loam soil and (B) on curve and straightaway areas in silt loam soil. Slopes and intercepts for regression models are shown in Table 3. Horizontal dashed lines represent upper and lower 95% confidence limits for H_0: estimate = 0. Disturbance response calculated as (disturbed measurement – undisturbed measurement)/undisturbed measurement; microbial biomass C in undisturbed control plots averaged 702 $\mu g\,g^{-1}$ soil for the silty clay loam soil and 838 $\mu g\,g^{-1}$ soil for the silt loam soil. Obs = observed, pred = predicted values.

Table 1
Repeated measures analysis of variance for microbial biomass C, nematode abundance, family richness, and structure index, and earthworm abundance in silty clay loam soil using year as a regression variable.[a].

Effect[b]	D.f.	F value				
		Microbial biomass C	Nematode abundance	Nematode family richness	Structure Index	Earthworm abundance
Treatment (T)	1, 6	19.10**	0.08	1.33	5.82	0.11
Intensity (I)	1, 6	0.05	0.55	0.18	0.06	0.85
$T \times I$	1, 6	3.36	0.08	0.42	0.60	0.87
Area (A)	1, 8	2.93	3.74	9.45*	10.16*	0.14
$T \times A$	1, 8	0.39	0.70	1.22	1.52	0.01
$I \times A$	1, 8	0.04	0.19	2.66	0.14	0.00
$T \times I \times A$	1, 8	0.27	0.13	0.03	2.03	0.02
Linear trend (Yr)	1, 64	27.72***	13.65***	9.97**	1.67	32.65***
Quadratic trend (Yr $\times$ Yr)	1, 64	NS	NS	7.22**	NS	NS
Yr $\times$ T	1, 64	4.41*	1.57	1.77	7.21**	11.29**
Yr $\times$ Yr $\times$ T	1, 64	NS	NS	2.27	NS	NS
Yr $\times$ I	1, 64	0.16	0.53	0.26	0.19	0.42
Yr $\times$ Yr $\times$ I	1, 64	NS	NS	0.92	NS	NS
Yr $\times$ T $\times$ I	1, 64	3.60	0.67	0.56	0.00	0.11
Yr $\times$ Yr $\times$ T $\times$ I	1, 64	NS	NS	0.25	NS	NS
Yr $\times$ A	1, 64	0.09	1.44	5.08*	4.35*	0.05
Yr $\times$ Yr $\times$ A	1, 64	NS	NS	1.97	NS	NS
Yr $\times$ T $\times$ A	1, 64	0.00	0.32	2.31	0.03	0.01
Yr $\times$ Yr $\times$ T $\times$ A	1, 64	NS	NS	3.73	NS	NS
Yr $\times$ I $\times$ A	1, 64	0.03	0.05	5.44*	0.01	0.04
Yr $\times$ Yr $\times$ I $\times$ A	1, 64	NS	NS	5.03*	NS	NS
Yr $\times$ T $\times$ I $\times$ A	1, 64	0.18	0.00	0.05	2.68	0.54
Yr $\times$ Yr $\times$ T $\times$ I $\times$ A	1, 64	NS	NS	0.55	NS	NS

NS: quadratic trends not significant, model fit with linear trends only.
[a] Based on a disturbance response calculated as (disturbed measurement – undisturbed measurement)/undisturbed measurement.
[b] Treatment: tank traffic during wet vs. dry soil conditions; intensity: single traffic (five passes in 2003) vs. repeated traffic (five additional passes in 2004); area: subplot from which sample was collected (curve vs. straightaway).
* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.

Table 2
Repeated measures analysis of variance for microbial biomass C, nematode abundance, family richness, and structure index, and earthworm abundance in silt loam soil using year as a regression variable.[a].

Effect[b]	D.f.	F value				
		Microbial biomass C	Nematode abundance	Nematode family richness	Structure Index	Earthworm abundance
Treatment (T)	1, 6	0.33	5.50	16.14**	3.30	0.50
Intensity (I)	1, 6	0.01	1.33	0.67	0.77	0.06
$T \times I$	1, 6	0.30	0.38	0.83	2.46	0.32
Area (A)	1, 8	0.28	8.14*	4.10	0.26	3.88
$T \times A$	1, 8	0.00	0.81	0.37	0.44	4.08
$I \times A$	1, 8	1.49	0.24	0.04	0.22	0.65
$T \times I \times A$	1, 8	2.04	0.04	0.54	0.27	0.22
Linear trend (Yr)	1, 64	28.69***	28.36***	3.46	6.96*	52.62***
Quadratic trend (Yr $\times$ Yr)	1, 64	NS	NS	0.70	6.77*	NS
Yr $\times$ T	1, 64	0.65	3.23	10.51**	2.40	0.41
Yr $\times$ Yr $\times$ T	1, 64	NS	NS	8.15**	1.20	NS
Yr $\times$ I	1, 64	0.90	1.71	0.59	0.50	5.36*
Yr $\times$ Yr $\times$ I	1, 64	NS	NS	0.40	0.10	NS
Yr $\times$ T $\times$ I	1, 64	1.19	0.41	0.61	3.04	0.72
Yr $\times$ Yr $\times$ T $\times$ I	1, 64	NS	NS	0.00	2.19	NS
Yr $\times$ A	1, 64	2.15	1.34	2.46	1.18	5.02*
Yr $\times$ Yr $\times$ A	1, 64	NS	NS	1.61	1.81	NS
Yr $\times$ T $\times$ A	1, 64	0.26	1.11	0.57	0.09	8.97**
Yr $\times$ Yr $\times$ T $\times$ A	1, 64	NS	NS	1.06	0.00	NS
Yr $\times$ I $\times$ A	1, 64	0.20	0.01	0.35	0.04	0.00
Yr $\times$ Yr $\times$ I $\times$ A	1, 64	NS	NS	0.39	0.50	NS
Yr $\times$ T $\times$ I $\times$ A	1, 64	3.17	0.20	0.69	0.44	0.85
Yr $\times$ Yr $\times$ T $\times$ I $\times$ A	1, 64	NS	NS	0.93	0.45	NS

NS: quadratic trends not significant, model fit with linear trends only.
[a] Based on a disturbance response calculated as (disturbed measurement - undisturbed measurement)/undisturbed measurement.
[b] Treatment: tank traffic during wet vs. dry soil conditions; intensity: single traffic (five passes in 2003) vs. repeated traffic (five additional passes in 2004); area: subplot from which sample was collected (curve vs. straightaway).
* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.

Table 3
Slope and intercept estimates for linear and quadratic trends in recovery of microbial biomass C, nematode abundance, family richness, and structure index, and earthworm abundance following M1A1 tank disturbance.[a].

Effect (treatment or area)[b]	Parameter estimates									
	Microbial biomass C		Nematode abundance		Nematode family richness		Structure Index		Earthworm abundance	
	Intercept	Slope	Intercept	Slope	Intercept	Slope	Intercept	Slope	Intercept	Slope
Silty clay loam soil										
Dry treatment	16.5	4.5	NS	NS	NS	NS	−55.8***	10.4**	−76.5*	41.2***
Wet treatment	−40.1*	18.3***					−26.1*	−1.1	−35.8	11.5
r^2	0.86				0.69	0.66				
Curve	NS	NS	−67.9**	22.3***	−58.9***	29.6*** / −4.7**,c	−59.3***	9.5*	NS	NS
Straightaway			−43.0*	22.3***	−30.6**	9.1 / −1.3c	−23.6*	−0.1		
r^2		0.87	0.85	0.84						
Silt loam soil										
Dry treatment	NS	NS	NS	NS	−8.2	9.5 / −1.1 c	−39.7	55.9* / −11.6*,c	NS	NS
Wet treatment					−59.1***	32.1*** / −4.1*,c	−37.0	55.9* / −11.6* c		
r^2					0.94	0.75				
Curve	−39.3***	14.3***	−67.6***	17.7***	NS	NS	NS	NS	−141.9**,d / −105.0*,e	84.1***,d / 43.9*,e
Straightaway	−14.3	14.3***	−39.6**	17.7***					−53.9 d / −100.2*,e	30.8 d / 48.9**,e
r^2	0.83	0.93				0.85				

NS: effect not significant.
  [a] Based on a disturbance response calculated as: (disturbed measurement - undisturbed measurement)/undisturbed measurement.
  [b] Treatment: tank traffic during wet vs. dry soil conditions; area: subplot from which sample was collected (curve vs. straightaway).
  [c] Quadratic trend.
  [d] Curve or straightaway areas of the dry soil treatment.
  [e] Curve or straightaway areas of the wet soil treatment.
  * $P \leq 0.05$.
  ** $P \leq 0.01$.
 *** $P \leq 0.001$ for H_0: estimate = 0.

reduction of 40% for microbial biomass C during wet conditions to an increase of 18% during dry conditions. Linear trends in recovery of microbial biomass following tank disturbance in silt loam soil were consistent across treatments, and an equal slope model indicated significant area effects ($P = 0.005$) with initial reductions in microbial biomass C of 39% (30% observed) for curve areas but only 14% (4% increase observed) for straightaway areas compared to that of undisturbed plots (Table 3, Fig. 1B). Estimates of microbial biomass in both soil types were greater ($P \leq 0.05$) than that for undisturbed plots by the 4th year following disturbance, regardless of treatment or area (Fig. 1). Trends for microbial biomass N were similar to those described for C and are not shown.

### 3.2. Soil invertebrate communities

3.2.1. Nematodes

Nematode densities in undisturbed control plots averaged 0.73 (0.39–1.14) million m^{-2} and 1.17 (0.44–2.01) million m^{-2} across years for the silty clay loam and silt loam soils, respectively. Family richness values for undisturbed plots in silty clay loam and silt loam soils averaged 12 (11–16) and 13 (11–16), respectively. Herbivorous taxa comprised 31% of total nematode densities on average and were represented predominantly by *Helicotylenchus* spp. Fungivorous (43% of total) and bacterivorous (16% of total) taxa were represented predominantly by *Filenchus* spp. and the Cephalobidae, respectively.

Regression models predicted reductions in nematode abundance of 68% (78–84% observed) on curve areas, but only 40 to 43% (33–41% observed) on straightaway areas, compared to undisturbed plots immediately following disturbance (Table 3, Fig. 2). Trends in recovery of total nematode abundance following tank
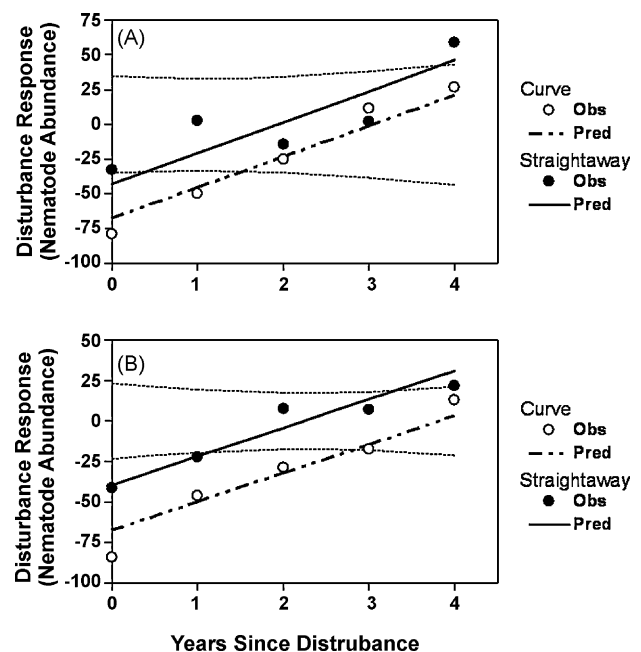
Fig. 2. Recovery trends for nematode abundance following Abrams M1A1 Main Battle Tank traffic on curve and straightaway areas in (A) silty clay loam soil and (B) silt loam soil. Slopes and intercepts for regression models are shown in Table 3. Horizontal dashed lines represent upper and lower 95% confidence limits for H_0: estimate = 0. Disturbance response calculated as (disturbed measurement – undisturbed measurement)/undisturbed measurement; nematode densities in undisturbed control plots averaged 0.73 million m^{-2} for the silty clay loam soil and 1.17 million m^{-2} for the silt loam soil. Obs = observed, pred = predicted values.
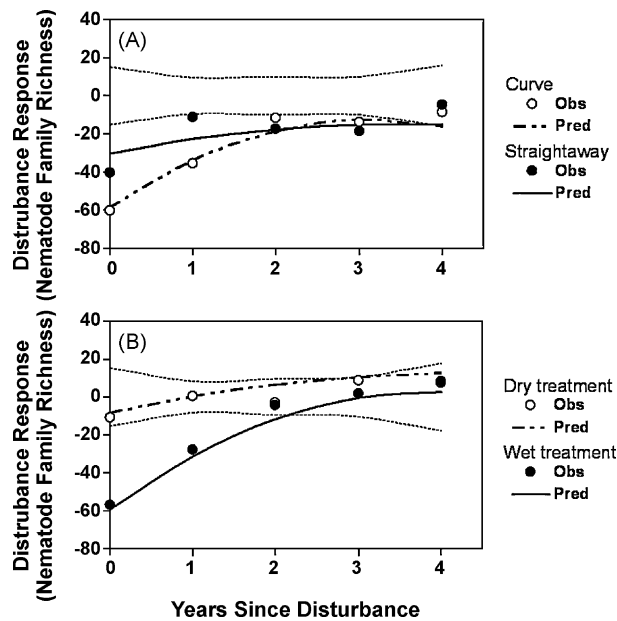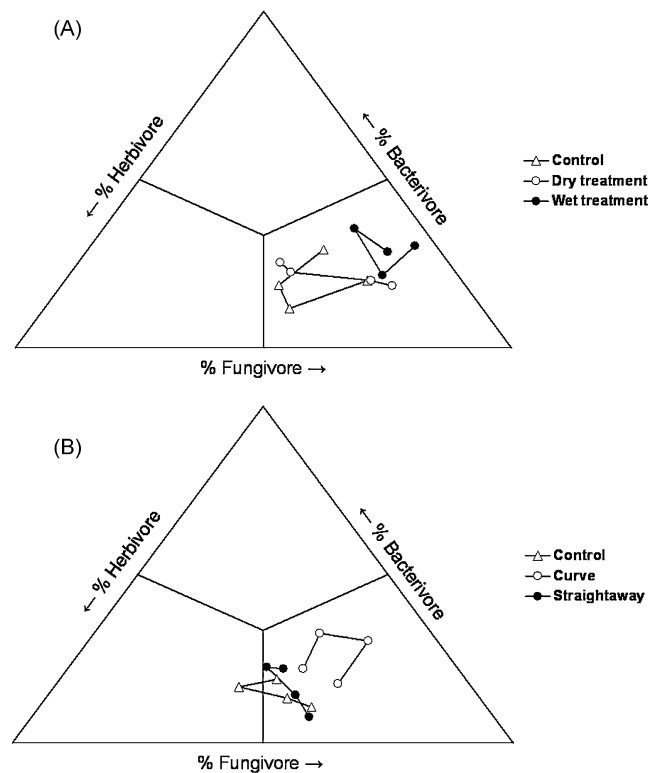
Fig. 3. Recovery trends for nematode family richness following Abrams M1A1 Main Battle Tank traffic (A) on curve and straightaway areas in silty clay loam soil and (B) during wet and dry soil moisture conditions in silt loam soil. Slopes and intercepts for regression models are shown in Table 3. Horizontal dashed lines represent upper and lower 95% confidence limits for H_0: estimate = 0. Disturbance response calculated as (disturbed measurement – undisturbed measurement)/undisturbed measurement; nematode family richness in undisturbed control plots averaged 12 for the silty clay loam soil and 13 for the silt loam soil. Obs = observed, pred = predicted values.

Fig. 4. Temporal changes in Enrichment Profile following Abrams M1A1 Main Battle Tank traffic (A) during wet and dry soil moisture conditions in silty clay loam soil and (B) on curve and straightaway areas in silt loam soil.

disturbance were similar between the two soil types, with consistent linear ($P \leq 0.001$) rates of recovery (18–22% per year) and area main effects ($P \leq 0.10$) observed for both (Tables 1 and 2). Recovery of nematode abundances on the more disturbed curve areas to undisturbed levels required 3 years for silt loam soil (Fig. 2B) but only 2 years for silty clay loam soil (Fig. 2A).

Initial reductions in family richness following tank disturbance, as well as subsequent rates of recovery, were greater ($P \leq 0.05$) for curve (59% predicted, 61% observed) compared to straightaway (31% predicted, 40% observed) areas in silty clay loam soil (Table 3, Fig. 3A). Family richness in both soil types displayed both linear and quadratic trends ($P \leq 0.05$) during recovery (Tables 1 and 2), with the rate of recovery slowing as richness values approached undisturbed control levels (Fig. 3). An interaction between traffic intensity and area ($P \leq 0.05$) also was indicated for both linear and quadratic effects (Table 1), with greater differences between curve and straightaway areas occurring for single than for repeated traffic (data not shown). In silt loam soil, initial reductions in family richness following tank disturbance, as well as linear and quadratic trends in recovery, displayed treatment effects (Table 2), with greater ($P \leq 0.01$) initial levels of disturbance and more rapid ($P \leq 0.01$) rates of recovery following disturbance in wet (initial reductions of 59% predicted, 57% observed) compared to dry (initial reductions of 8% predicted, 11% observed) soil moisture conditions (Table 3, Fig. 3B). Nematode family richness remained significantly reduced ($P \leq 0.05$) compared to undisturbed plots through the third year following tank disturbance in silty clay loam soil but recovered relatively rapidly in silt loam soil (Fig. 3).

Enrichment profiles of nematode communities for 2004–2006 displayed separation of the wet traffic treatment from both the dry traffic treatment and the undisturbed control in silty clay loam soil (Fig. 4A) and of the curve area from both the straightaway and undisturbed control in silt loam soil (Fig. 4B). These effects were driven by lower herbivore abundances and higher fungivore abundances during the recovery period for the wet traffic

treatment in silty clay loam soil and for curve areas in silt loam soil. Fungivores and bacterivores increased rapidly to densities greater ($P \leq 0.05$) than those in undisturbed plots, while herbivore densities remained at or below undisturbed levels (data not shown).

Modeling the structure index as a polynomial function of time indicated a difference in initial disturbance levels between track areas, and additive effects ($P \leq 0.05$) of soil moisture condition during tank traffic and track area on linear rates of recovery, in silty clay loam soil (Table 1). Initial levels of disturbance, as well as subsequent rates of recovery, were greater ($P \leq 0.05$) for dry (initial reductions of 56% predicted, 49% observed) than for wet (initial reductions of 26% predicted, 35% observed) traffic conditions and for curve (initial reductions of 59% predicted, 59% observed) than for straightaway (initial reductions of 24% predicted, 23% observed) areas (Table 3, Fig. 5). Initial reductions of 38% (40% observed) were predicted for the structure index in silt loam soil, with recovery exhibiting uniform linear and quadratic trends across treatments and areas (Tables 2 and 3).
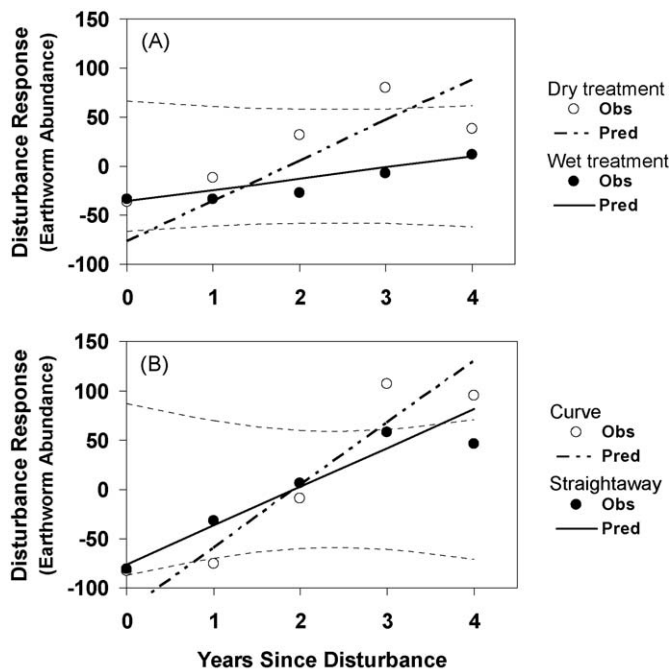
3.2.2. Earthworms

Earthworm communities consisted of both native (*Diplocardia* spp. and *Bimastos welchi*) and introduced European (*Aporrectodea trapezoides* and *Eisenia rosea*) species. Total numbers of earthworms in undisturbed control plots averaged 17 (5–30) and 65 (23–130) individuals m^{-2} in silty clay loam and silt loam soils, respectively.

Initial levels of disturbance were severe in both soils, with models predicting large reductions in earthworm densities in the upper 7.6 cm soil depth immediately following tank traffic (Table 3, Fig. 6). Estimates of initial reductions ranged from 36–77% (33–36% observed) in silty clay loam soil and 54–100% (81–82% observed) in silt loam soil. Earthworm abundance in disturbed
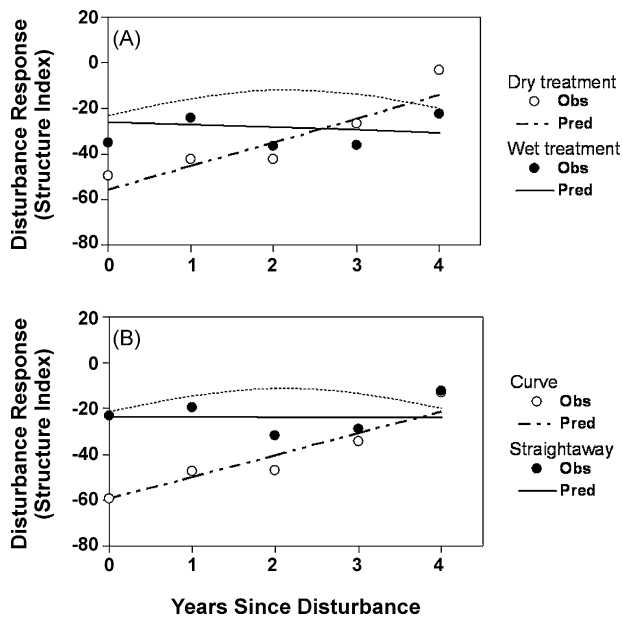
Fig. 5. Recovery trends for the structure index following Abrams M1A1 Main Battle Tank traffic in silty clay loam soil (A) during wet and dry soil moisture conditions and (B) on curve and straightaway areas. Slopes and intercepts for regression models are shown in Table 3. Horizontal dashed lines represent lower 95% confidence limits for H_0: estimate = 0. Disturbance response calculated as (disturbed measurement − undisturbed measurement)/undisturbed measurement; Structure Indices in undisturbed control plots averaged 77 for the silty clay loam soil and 51 for the silt loam soil. Obs = observed, pred = predicted values.

tank tracks exhibited linear recovery trends that varied with moisture condition in silty clay loam soil (Table 1), and with moisture condition, traffic intensity, and area in silt loam soil

Fig. 6. Recovery trends for earthworm abundance following Abrams M1A1 Main Battle Tank traffic (A) during wet and dry soil moisture conditions in silty clay loam soil and (B) on curve and straightaway areas in silt loam soil. Slopes and intercepts for regression models are shown in Table 3. Horizontal dashed lines represent upper and lower 95% confidence limits for H_0: estimate = 0. Disturbance response calculated as (disturbed measurement − undisturbed measurement)/undisturbed measurement; total numbers of earthworms in undisturbed control plots averaged 17 individuals m^{-2} for the silty clay loam soil and 65 individuals m^{-2} for the silt loam soil. Obs = observed, pred = predicted values.

(Table 2). Earthworm recovery in silty clay loam soil was rapid for the dry traffic treatment, with estimated numbers of earthworms exceeding ($P \leq 0.05$) undisturbed numbers in the fourth year following disturbance, while numbers of earthworms associated with the dry traffic treatment remained similar to the undisturbed control (Fig. 6A). Earthworm recovery in silt loam soil was more rapid ($P \leq 0.05$) for curve compared to straightaway areas following dry, but not wet traffic conditions (Table 3, Fig. 6B). Recovery in this soil also was more rapid following repeated traffic compared to a single traffic event (data not shown).

4. Discussion

Tallgrass prairie soil biotic communities exhibited significant sensitivity to tank traffic, with measurable effects still present after 3 years in plots with the greatest level of disturbance. Vehicle traffic exerts multiple impacts on the soil ecosystem, including destruction of vegetation, displacement of topsoil along with accompanying soil organic matter, and compaction, which in turn reduces water infiltration and water-holding capacity (Prosser et al., 2000; Grantham et al., 2001; Raper, 2005). Additionally, bare soil is susceptible to greater temperature and moisture fluctuations. All of these effects likely combined to produce the patterns of disturbance and recovery observed for the soil organisms in this study. Microbial biomass, for example, responds rapidly to changes in soil organic matter and to environmental fluctuations (Rice et al., 1996, 1998). Throughout the present study, microbial biomass estimates closely reflected the status of total soil C and, therefore, soil organic matter (Althoff, 2007), suggesting that resource availability was the primary driver. Significant increases in microbial biomass C relative to undisturbed levels were observed within a few years of disturbance, particularly for dry treatments and straightaway areas. Much of the substrate in soils is unavailable to microorganisms due to physical protection mechanisms (e.g., aggregation) and disturbance releases these substrates, resulting in a flush of nutrients through decomposition (Watts et al., 2000). Another potential mechanism for increased microbial biomass following traffic disturbance is the observation that, while compaction reduces macropores ($> 30 \mu$m diameter), micropores (0.2–30 μm diameter) are increased. The latter comprise the habitable-sized pores for microorganisms (Shestak and Busse, 2005). Regardless of the mechanism, it is important to note that microbial community composition continued to exhibit disturbance effects after recovery of microbial biomass, with Gram-positive bacteria favored over Gram-negative bacteria during the recovery process (Althoff, 2007).

Nematode community composition similarly reflected resource availability, with herbivorous root-feeding taxa displaying greater initial disturbance effects and slower recovery than fungivorous and bacterivous taxa. This pattern reflects the greater severity of damage observed for vegetation than for the microbial community. For example, aboveground plant biomass was removed entirely from tank tracks during traffic events (Althoff, 2005) but reductions in microbial biomass never exceeded 40%. Herbivores typically comprise 30–40% of the tallgrass prairie nematode community (Ransom et al., 1998; Blair et al., 2000) and are responsive to changes in both the quantity and quality of root inputs (Rice et al., 1998; Blair et al., 2000). In the present study, herbivores averaged 31% of total nematode abundance in undisturbed plots but comprised only 11–12% of total nematode abundance in the most severely disturbed plots (e.g. wet traffic conditions and curve areas). Nematode community structure also reflects changes in the microbial community, and a measure of the relative abundances of herbivorous, fungivorous, and bacterivorous taxa serves as a useful indicator of soil food web status (Ferris et al., 2001; Ferris and Bongers, 2006). Nematode assemblages of the tallgrass prairie characteristically display low relative abundances of bacterivores

compared to the other trophic groups (Todd, 1996; Todd et al., 2006). During the recovery process reported in this study, however, microbial-feeding taxa increased in abundance faster than herbivorous taxa, resulting in an inversion in relative abundances of these two groups in wet treatments and curve areas that was still evident at the end of the study. This observation not only is consistent with the microbial and plant responses discussed above, but also reflects the shorter life cycles and more rapid population growth of microbivores compared to herbivores (Ferris and Bongers, 2006). In addition to trophic composition, taxonomic diversity also was a sensitive indicator of M1A1 tank traffic effects, with prolonged reductions in nematode family richness observed in silty clay loam soil. Previous research supports the use of this index for assessing soil conditions on military lands (Althoff et al., 2007).

Earthworms were nearly eliminated from disturbed areas following tank traffic but generally recovered rapidly and even increased in abundance relative to undisturbed areas. Vegetation destruction, litter removal along with the accompanying changes in soil moisture and temperature regime, and soil compaction likely combined to produce the dramatic responses observed for this group. As was suggested for the soil microbes, earthworms appeared to be able to exploit newly available organic matter (e.g. dead roots) and the flush of soil nutrients resulting from intensified decomposition following traffic disturbance. Given the important effects that earthworms have on soil structure (Tomlin et al., 1995; Edwards and Bohlen, 1996), their status has particularly significant implications for recovery of the soil ecosystem. Furthermore, it has been shown that differing land management practices can either favor or limit expansion of exotic earthworm species in tallgrass prairie (Callaham et al., 2003), with unknown consequences. Differences in feeding ecology and behavior are known to exist between native and exotic earthworm species (James and Cunningham, 1989; Callaham et al., 2001), suggesting that the two groups are not interchangeable. Where native and exotic species coexist, their combined effects are determined by their relative abundance, fitness, and differences in ecological strategies (James and Hendrix, 2004). Exotic taxa are abundant on Fort Riley, but the full impact of military training activities on earthworm community structure and the implications for ecosystem processes remain to be determined.

Similar disturbance responses were documented for the diverse soil biotic communities in this study. Disturbance was consistently greater on curve areas and for tank traffic during wet soil conditions, a pattern also reported for plant communities (Althoff, 2007) and soil physical and chemical properties (Althoff, 2007). The relative importance of treatment conditions and track area varied, however, with soil type and disturbance measurement. For instance, effects on microbial biomass were strongly influenced by soil water content at the time of disturbance in silty clay loam soil but not in silt loam soil, while nematode family richness exhibited the opposite trend. This observation indicates that no single measurement can provide a complete assessment of disturbance and recovery in soil biotic communities.

Soil microbes and fauna display characteristic and predictable responses to physical, chemical, and biological (i.e. food resource) changes in their environment brought on by perturbation (Nannipieri et al., 1990; Rice et al., 1996; Neher, 2001). In contrast to Shestak and Busse (2005), who reported tolerance of microbial communities to compaction in forest ecosystems and a poor link between physical and biological indices of soil health, we found that microbial and invertebrate communities in tallgrass prairie were sensitive indicators of ecosystem impacts due to military training activities. Assessment of soil fauna provides several advantages over assessment of microbial communities because higher trophic levels in the soil food web are reflected, fauna generally are easier to assess, and faunal populations are relatively stable compared to microbial

populations (Neher, 2001). In this study, nematode community structure provided a reliable and comprehensive assessment of the status of the soil food web and represents an effective bioindicator for military training land mangers. In addition, given the dominant role of earthworms in ecosystem processes, it is recommended that this group be included in monitoring protocols. The recovery models developed in this study provide a basis for developing guidelines for the assessment of training conditions and the management of vehicle impacts on military lands in grassland ecosystems.

Acknowledgements

References

Althoff, D.P., Althoff, P.S., Lambrecht, N.D., Gipson, P.S., Pontius, J.S., Woodford, P.B., 2007. Soil properties and perceived disturbance of grasslands subjected to mechanized military training: evaluation of an index. Land Degrad. Dev. 18, 269–288.

Althoff, D.P., Gipson, P.S., Pontius, J.S., Woodford, P.B., 2006. Plant community and bare ground trends on Fort Riley, Kansas: Implications for monitoring of a highly disturbed landscape. T. Kansas Acad. Sci. 109, 101–106.

Althoff, P.S. 2005. Evaluation of soil quality indicators following disturbance by an Abrams M1A1 Main Battle Tank. M.S. Thesis. Kansas State University, Manhattan, KS, 136 pp.

Althoff, P.S. 2007. Indicators of disturbance and recovery of a tallgrass prairie ecosystem following military vehicle traffic. Ph.D. Dissertation. Kansas State University, Manhattan, KS, 230 pp.

Althoff, P.S., Thien, S.J., 2005. Impact of M1A1 main battle tank disturbance on soil quality, invertebrates, and vegetation characteristics. J. Terramechanics 42, 159–176.

Anderson, A.B., Palazzo, A.J., Ayers, P.D., Fehmi, J.S., Shoop, S., Sullivan, P., 2005. Assessing the impacts of military vehicle traffic on natural areas. Introduction to the special issue and review of the relevant military vehicle impact literature. J. Terramechanics 42, 143–158.

Army Regulation 350-4. 1988. Integrated Training Area Management (ITAM). Unclassified. Headquarters Department of the Army Washington, DC.

Blair, J.M., Todd, T.C., Callaham Jr., M.A., 2000. Responses of grassland soil invertebrates to natural and anthropogenic disturbances. In: Coleman, D.C., Hendrix, P.F. (Eds.), Invertebrates as Webmasters in Ecosystems. CABI Publishing, NY, pp. 43–71.

Callaham Jr., M.A., Blair, J.M., Todd, T.C., Kitchen, D.J., Whiles, M.R., 2003. Macroinvertebrates in North American tallgrass prairie soils: effects of fire, mowing, and fertilization on density and biomass. Soil Biol. Biochem. 35, 1079–1093.

Callaham Jr., M.A., Blair, J.M., 1999. Influence of differing land management on the invasion of North American tallgrass prairie soils by European earthworms. Pedobiologia 43, 507–512.

Callaham Jr., M.A., Blair, J.M., Hendrix, P.F., 2001. Different behavioral patterns of the earthworms Octolasion tyrtaeum and Diplocardia spp. in tallgrass prairie soils: potential influences on plant growth. Biol. Fert. Soils 34, 49–56.

Daubenmire, R., 1959. Measurement of species diversity using canopy coverage classes. Northwest Sci. 33, 43–66.

Edwards, C.A., Bohlen, P.J., 1996. Biology and Ecology of Earthworms. Chapman & Hall, London, 440 pp.

Elliott, E.T., Hunt, H.W., Walter, D.E., 1988. Detrital foodweb interactions in North American grassland ecosystems. Agr. Ecosyst. Environ. 24, 41–56.

Ferris, H., Bongers, T., 2006. Nematode indicators of organic enrichment. J. Nematol. 38, 3–12.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13–29.

Grantham, W.P., Redente, E.F., Bagley, C.F., Paschke, M.W., 2001. Tracked vehicle impacts to vegetation structure and soil erodibility. J. Range Manage. 54, 711–716.

Hayden, B.P., 1998. Regional climate and the distribution of tallgrass prairies. In: Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L. (Eds.), Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, NY, pp. 19–34.

James, S.W., Cunningham, M.R., 1989. Feeding ecology of some earthworms in Kansas tallgrass prairie. Am. Midl. Nat. 121, 78–83.

James, S.W., 1995. Systematics, biogeography, and ecology of nearctic earthworms from eastern, central, southern, and southwester USA. In: Hendrix, P.F. (Ed.), Earthworm Ecology and Biogeography in North America. Lewis Publication, Boca Raton, FL, pp. 29–51.

James, S.W., Hendrix, P.F., 2004. Invasion of exotic earthworms into North America and other regions. In: Edwards, C.A. (Ed.), Earthworm Ecology. CRC Press, Boca Raton, FL, pp. 75–88.

Jantz, D.R., Harner, R.F., Rowland, H.T., Gier, D.A., 1975. Soil Survey of Riley and Part of Geary County, Kansas. Soil Conservation Service, USDA, Washington, D.C., in cooperation with the Kansas Agricultural Experiment Station, Manhattan, KS.

Jenkins, W.R., 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Dis. Rep. 48, 692.

Jenkinson, D.S., Powlson, D.S., 1976. The effects of biocidal treatments on metabolism in soil: fumigation with chloroform. Soil Biol. Biochem. 8, 167–177.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Knapp, A.K., Seastedt, T.R., 1998. Grasslands, Konza Prairie, and long-term ecological research. In: Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L. (Eds.), Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, NY, pp. 3–15.

Linden, D.R., Hendrix, P.F., Coleman, D.C., van Vliet, P.C.J., 1994. Faunal Indicators of soil quality. In: Doran, J.W., et al. (Eds.), Defining Soil Quality for a Sustainable Environment. SSSA Special Publication 35, pp. 91–106.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS System for Mixed Models. SAS Institute Inc., Cary, NC, 633 pp.

Loveland, P.J., Thompson, T.R.E., 2001. Identification and development of a set of national indicators for soil quality. In: R&D Technical Report P5-053/2/TR, Bristol Environmental Agency.

Maire, N.D., Borcard, D., Laczko, E., Matthey, W., 1999. Organic matter cycling in grassland soils of the Swiss Jura mountains: biodiversity and strategies of the living communities. Soil Biol. Biochem. 31, 1281–1293.

McKale, W., Young, W.D., 2000. Fort Riley Citadel of the Frontier West. Kansas State Historical Society, Topeka, KS.

Nannipieri, P., Grego, S., Ceccanti, B., 1990. Ecological significance of the biological activity in soil. In: Bollag, J.-M., Stotzky, G. (Eds.), Soil Biochemistry, vol.6. Marcel Dekker, New York, pp. 293–355.

Neher, D.A., 2001. Role of nematodes in soil health and their use as indicators. J. Nematol. 33, 161–168.

Pride, W.F., 1997. The History of Fort Riley. U.S. Cavalry Museum and Fort Riley Historical and Archaeology Society, Manhattan, KS.

Prosser, C.W., Sedivec, K.K., Barket, W.T., 2000. Tracked vehicle effects on vegetation and soil characteristics. J. Range Manage. 53, 666–670.

Ransom, M.D., Rice, C.W., Todd, T.C., Wehmueller, W.A., 1998. Soils and soil biota. In: Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L. (Eds.), Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, NY, pp. 48–66.

Raper, R.L., 2005. Agricultural traffic impacts on soil. J. Terramechanics 42, 259–280.

Rice, C.W., Moorman, T.B., Beare, M., 1996. Role of microbial biomass carbon and nitrogen in soil quality. In: Doran, J.W., Jones, A.J. (Eds.), Methods for Assessing Soil Quality. SSSA Special Publication 49, Madison, WI, pp. 203–215.

Rice, C.W., Todd, T.C., Blair, J.M., Seastedt, T.R., Ramundo, R.A.G., Wilson, W.T., 1998. Belowground biology and processes. In: Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L. (Eds.), Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, NY, pp. 244–264.

Ritz, K., McHugh, M., Harris, J., 2004. Biological diversity and function in soils: contemporary perspectives and implications in relation to the formulation of effective indicators. In: Francaviglia, R. (Ed.), Agricultural Impacts on Soil Erosion and Soil Biodiversity: Developing Indicators for Policy Analysis OECD Expert Meeting on Soil Erosion and Soil Biodiversity Indicators. Istituto Sperimentale per la Nutrizione delle Piante, Rome, pp. 563–572.

SAS Institute Inc., 2000. SAS/STAT User's Guide. Version 6.03. SAS Institute Inc., Cary NC, USA, 1028 pp.

Schaeffer, D.J., Seastedt, T.R., Gibson, D.J., Hartnett, D.C., James, S.W., Kaufman, D.W., Schwab, A.P., Herricks, E.E., Novak, E.W., 1990. Field bioassessments for selecting test systems to evaluate military training lands in tallgrass prairie. Ecosystem Health. V. Environ. Manage. 14, 81–93.

Shestak, C.J., Busse, M.D., 2005. Compaction alters physical but not biological indices of soil health. Soil Sci. Soc. Am. J. 69, 236–246.

Todd, T.C., 1996. Effects of management practices on nematode community structure in tallgrass prairie. Appl. Soil Ecol. 3, 235–246.

Todd, T.C., Powers, T.O., Mullin, P.G., 2006. Sentinel nematodes of land-use change and restoration in tallgrass prairie. J. Nematol. 38, 20–27.

Tomlin, A.D., Shipitalo, M.J., Edwards, W.M., Protz, R., 1995. Earthworms and their influence on soil structure and infiltration. In: Hendrix, P.F. (Ed.), Earthworm Ecology and Biogeography in North America. Lewis Publication, Boca Raton, FL, pp. 159–183.

US Army Environmental Center, 2006. Sustainable range program: Range and training land assessment program. https://srp.army.mil/itam/rtla.

Watts, C.W., Eich, S., Dexter, A.R., 2000. Effects of mechanical energy inputs on soil respiration at the aggregate and field scales. Soil Till. Res. 53, 231–243.

Yeates, G.W., Bongers, T., de Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera—an outline for soil ecologists. J. Nematol. 25, 315–331.